

ON THE DEVELOPMENT OF SOME GYNOECEIA WITH SEPTAL NECTARIES

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SUMMARY

Septal nectaries are formed by local regions of later nectariferous epidermal cells on the sides of the carpels at their very base. In order that the epidermal cells may differentiate into nectariferous cells, the carpels which constitute the gynoecium have to develop as separate organs. It was argued that if no septal nectaries develop, this free carpel development does not take place. The nectariferous regions get shaped as nectar containers by dermal fusion of the sides of the carpels surrounding them, by upward growth of the apex, and mostly also by meristematic continuity of part of the ovary wall on the outside. By the latter the level of the openings of the nectaries on the ovary is defined. Septal nectaries in Monocotyledons are considered original.

INTRODUCTION

This study is part of my work on the development of gynoecia in Angiosperms as observed in the scanning electron microscope. Septal nectaries occur in Monocotyledons only. The development of the gynoecia is described in so far as relevant to the origin of septal nectaries. An important contribution on septal nectaries was published by Daumann (1970). As most earlier publications are reviewed in that work, I will not regularly cite these papers. Also I leave out anatomy, as anatomy will be treated by Rudolf Schmid (Berkeley) in a future extensive review on septal nectaries. Furthermore my investigation is restricted to superior gynoecia.

MATERIALS AND METHODS

Most plants were derived from the Botanic Gardens at Amsterdam, Haren, Leiden, and Wageningen, to wit *Alisma plantago-aquatica* L., *Allium fistulosum* L., *Bulbine annua* Willd., *Butomus umbellatus* L., *Costus speciosus* (Koen.) Sm., *Dracaena surculosa* Lindl., *Eichhornia paniculata* (Spreng.) Solms-Laub., *Gloriosa superba* L., *Hemerocallis fulva* L., *Kniphofia spec.*, *Ornithogalum caudatum* Jacq., *Pontederia cordata* L., *Sansevieria zeylanica* Willd., *Tofieldia calyculata* (L.) Wahlenb., and *Veratrum nigrum* L. *Asphodelus fistulosus* L. came from natural habitats near Malaga; more of *Tofieldia calyculata* was collected in Switzerland (Mt Rossberg, Arth-Goldau). The material of *Arenga pinnata* Merr. was collected near Bandung (Java), and that of *Salacca edulis* Reinw. near Bogor (Java). I acknowledge

the kind cooperation in collecting these plants by Dr. J.J. Bos (Wageningen), Prof. P.K. Endress (Zürich), Dr. E.B. Hidajat (Bandung), J.P. Mogeia (Bogor), and Dr. R. van der Meijden (Leiden).

The scanning work was executed after fixation of the primordia in F.A.A., critical-point drying in carbon dioxide and gold sputter-coating. The microtome sections were stained in Saffranin and Astrablue.

RESULTS

***Alisma plantago-aquatica* (Fig. 71)**

The septal nectaries have been described by Daumann (1964). The nectar is secreted by the epidermal cells of the lateral sides of the carpels at the very base. Between two adjacent carpels basal slits occur which are bordered on the inside by the apex of the flower and on the outside by the adherence of epidermal cells of the carpels at the base (fig. 1). The latter closure only occurs between carpels that are closely adjacent. These are the carpels along the sides of the slightly triangular gynoecium. The carpels in the corner regions stand wide apart. As a result nectar slits are wide open to the outside diagonally upwards. Presumably nectar can be contained in the cup-shaped common base of calyx and stamens surrounding the gynoecium.

The position of each nectary corresponds with the primary development of the gynoecium as described earlier (Van Heel, 1983). The carpel primordia are strikingly lateral on an upward expanding apex. These primordia differentiate into a basal socle and a locule above (cf. *Magnolia*). Later the lateral epidermal cells of the socle in part differentiate into nectariferous cells, in part – the basal peripheral ones – they may loosely adhere in a zigzag pattern so as to close the nectary slit on the outside. At the level of the locule nectariferous cells are absent.

***Butomus umbellatus* (Fig. 72)**

The first correct descriptions of the nectaries were given by Böhmker (1917). There are six slits, as deep as the locules, between six ovaries that are fused only basally. The secretion occurs in the lower parts of the slits only, but presumably the nectar moves upwards in the slits towards where the ovaries separate. Daumann (1970) reported 'inner nectaries' between the proximally fused carpels, which consist of the secreting epidermides of adjacent carpels.

From S.E.M. photographs it appeared that the floral apex enlarges considerably during early development of the free carpel primordia, especially in width (Van Heel, 1983). At the same time the primordia increase in radial extent, so that conspicuous carpellary flanks develop. This special development results in the juxtaposition of carpellary flanks, creating the space for the nectary (and similarly for numerous facial ovules).

As the young carpels are inserted in a circular depression of the apex, the nectary slits are well bordered centrally as well as peripherally, forming narrow containers

which are wide open diagonally upwards. The circular depression is caused 1) by the floral apex being higher centrally during carpel development, 2) by a late meristematic upgrowth underneath the outer walls of the gynoecium (fig. 2). This last feature has been described by Eber (1934, 'periphere Berindung'), and Singh & Sattler (1974). The walls of the epidermal cells in the distal region of the slits, through which the nectar merely flows outwards, show very fine parallel longitudinal ridges. These ridges are also found on the outer wall of the gynoecium below, and on the filaments. They might help in guiding or fixing the nectar.

Finally the epidermal cells of the flanks and margins of adjacent carpels fuse upwards centrally, delimiting the nectary spaces on the inside. This may prevent the nectar from flowing toward the centre of the gynoecium, and keep it near the base of the androecium. Also the locules close by epidermal fusion centrally in the locular radii.

Tofieldia calyculata (Fig. 73)

Sterling (1979) described the gynoecium of *Pleea* in a paper on Liliaceae-Tofieldiaceae. His description may fit *Tofieldia* also. El Hamidi (1952), examining transverse sections, did not pay attention to the septal nectaries, although the figures show the star-shaped space of the common nectary.

Baum (1949) stated that the carpels are initially free from each other, but fuse postgenitally. However, El Hamidi and Sterling have noted that the carpels are free at the base, and Sterling associated this with the presence of a nectary. Sterling specified (for *Pleea*): 'each of the three narrow septal glands extends from the centre of the base of the pistil, diagonally outwards, and up to the outer base of the pistil along the line of a septum.' This exactly corresponds with my observations in *Tofieldia*.

Thus in *Tofieldia* there is a triradiate common nectarial cavity at the very base between the ascidiform carpels (figs. 3–5). The nectary is delimited below by the slightly concave flower base, and above finally by the complete dermal fusion of the flanks of the ovaries in alternate radii (figs. 67–70).

Daumann (1970) described the nectaries differently. According to him the nectar is secreted on the entire surface of the pistil, which is probably incorrect. Maybe nectar is only transported along the wall of the gynoecium by capillarity. Anatomical indication is given by numerous parallel longitudinal cuticular ridges which cover the epidermal cells on the lower parts of the gynoecium surface and the filaments, like in *Butomus*. The exact presentation of the nectar should be checked in the field. Immediately above the relatively wide slit-like openings of the nectaries, the adjacent carpels form short narrow grooves, not secreting, that are also lined with cuticular ridges and may guide or fix nectar.

Arenga pinnata (Fig. 74)

Originally this palm was thought to be wind pollinated. However, Uhl & Moore (1971, figs. 7 & 113) figured a septal nectary. They described the nectary for the closely similar *Latania* as a triradiate basal cavity which separates diagonally upwards

into three canals opening through pores. Uhl & Moore also reported a basal triradiate septal nectary in *Corypha* and *Paralinospadix*. A similar septal nectary was described in *Asterogyne* by Schmid (1983). My observations show that such a nectary also occurs in *Arenga pinnata*. Hidajat (1976) described the pores of gynoeceal nectaries in *Arenga pinnata*.

Data on the development of gynoecea in palms are scarce, and even scarcer as regards the septal nectaries. I made transverse sections of a young gynoeceum, which substantiate the drawings by Uhl & Moore. The canals terminate into short slits on the surface of the gynoeceum. Neither the slits nor the ends of the canals are lined with nectariferous cells. The nectar secreting part of the common nectary is internal. There is no connection with the locules centrally because the margins of each carpel adhere and fuse dermally at an early stage. The young fruit of *Arenga* is globular with three crests extending into stigmatic peaks. Three openings of the septal nectaries are situated near the base of the stigmatic peaks alternating with them (fig. 8).

Very young gynoecea, measuring just over one millimetre, show three separate carpels which are raised together on a common base. At this stage the dermal fusion of the radial faces of the young carpels is beginning (fig. 6). However, if one carpel is isolated, by severing the two others, it turns out that fusion of the free carpel flanks is absent at the very base. This marks the origin of each of the three diagonal nectary parts which reach from the centre below to the surface of the gynoeceum upwards like canals (fig. 7). Above this diagonal canal dermal fusion between adjacent carpel flanks starts and proceeds upwards, uniting the ovary parts but leaving free the stigmatic parts.

The diagonal position of the nectary parts corresponds with the bowl-shaped base of the gynoeceum and the free carpel parts together. This cavity is caused by meristematic fusion in septal radii and zonal growth underneath the originally free outer walls of the carpel primordia. The common wall of the gynoeceum gradually increases in height, so that the nectary openings are shifted upwards. As a consequence also the ovules when they develop are lodged in a deepening cupular container. It would be interesting to investigate more fully the correlations between the developing structure, nectar secretion, and pollination (Hidajat, 1987).

***Asphodelus fistulosus* (Fig. 75)**

Daumann (1970) concluded that there are three large internal nectaries which narrow into a canal and end upwards into a widening mouth at about two thirds the height of the ovary. The terminal part of the nectary is not nectariferous, and I have not observed any grooves on the outside of the ovary. Possibly nectar is fixed in the multitude of hairs at the broad bases of the stamens.

The gynoeceum structure has been described by Leinfellner (1950) and El Hamidi (1952) from transverse sections. The latter stated that the septal nectaries are demarcated on the inside and on the outside by fusion of gynoeceum parts, to be precise by congenital fusion below and by postgenital fusion above.

S.E.M.-photographs reveal that the floral apex, distinctly present above the young stamens, differentiates into three separate ascidiform carpels (figs. 9–11).

The abaxial region of a carpel primordium arises first, the adaxial region follows. As in the meantime the growth of the apex is continued, the adaxial region arises higher on the apex. Between the three adaxial carpellary regions a triangular residual apex is observed (fig. 12). Then the three carpel primordia are raised together, especially on the periphery, as they are fused by a basal zonal meristem. At that stage the spaces for the septal nectaries are evident between the primordial carpels. The spaces are bordered centrally by the apex, which takes part in the upward growth, and on the outside by the gynoecial wall that connects the carpels below (fig. 13).

Then the carpels continue to grow upwards, especially in the abaxial regions. And as the median adaxial regions are slowing down 'carpel margins' result that are vertical (fig. 14). Two lateral ovules which will be arillate later originate basally on the inside of the margins basally.

The young carpels are subdivided into a stylar-stigmatic part above and an ovarial part below. At about the border between these parts the margins of the three carpels grow inwards, adhere, and fuse dermally, in that way closing the spaces for the septal nectaries as well as the locules (fig. 15). Also the margins of the stylar parts fuse dermally, closing the septal slits above, except for the openings of the nectaries (fig. 16). A hollow stylar cylinder is left in the middle. On the locule side the carpel margins develop into a protuberant mass of cells corresponding with the original U-shaped form of the adaxial region of the carpel primordia (fig. 17). This represents pollen conducting tissue.

Consequently, the septal spaces for the nectaries are closed by cupular growth of the wall and the growth of the apex below and by dermal fusion of carpellary lateral regions above. The development in *Asphodeline lutea* appeared very similar.

Ornithogalum caudatum (Fig. 76)

Daumann (1970) reported three internal septal nectaries. They open to the outside each by a pore in the distal part of the ovary wall. Three sutural grooves lead from the pores to the base of the gynoecium (fig. 18).

In an anatomical study Tilton & Horner (1983) described two zones of fusion in the developing gynoecium, zone 1 along the base of the abaxial surface of adjacent carpels, and zone 2 along the margins of the carpels. They observed that the fusion between the adjacent carpels is incomplete in the radial plane. Chambers result in the region of the septum between the two zones of fusion, the epidermal cells of which later become secretory. The final formation of a grooved ridge to the exterior of the suture is also recorded. However, Tilton & Horner did not mention the difference between meristematic (zone 1) and epidermal (zone 2) fusion. Moreover, zone 1 does not extend to the tip of the style as the authors stated, but terminates below the pores of each nectary. The stylar parts, above the pore, belong to zone 2, that is, they fuse dermally later. In that way the septal nectary occupies the entire border between the two zones of different fusion.

Figures 19 and 20 show that the wall of the gynoecium, in the sutural radii, initiated by early meristematic continuity, rises up to about the distal level of the ovary, while the marginal parts of the carpels are still free, also below. The latter fuse der

mally in the centre later. Figure 23 presents a similar critical stage in *Kniphofia spec.* Later epidermal fusion is indicated in fig. 21. Figure 22 presents a transverse section of the gynoeceal wall showing the septal nectary and the top part of the outer groove, just below their level of confluence at the pore of the nectary.

Allium fistulosum (Fig. 77)

De Wilde-Duyfjes (1976) found that the size relations of nectaries, canals, and openings are characteristic for the sections of the genus. The ultimate shape of the gynoeceum is complicated by an additional outward growth of the ovaries which leads to a basal position of the style. A description of young and mature stages was given by Hartl & Severin (1981). They concluded that the tissue of the carpels between septal nectary and affluent outer groove is congenital, but that the closure of the septal nectary on the inside occurs postgenitally. My results for *Allium fistulosum* concur with their conclusions which were derived from *Allium schoenoprasum*.

The carpels originate freely on a small triangular apex surrounded by the stamen primordia. This apex is slightly concave and is raised along the border early also in alternate radii (fig. 24). The lack of strong further growth in the area of meristematic continuity, connecting the carpels, causes the openings of the nectaries to remain low above the base-line of the gynoeceum.

The carpel primordia develop further inwards, as usually into a horseshoe shape. Finally, the margins of each carpel become continuous adaxially, giving rise to three ascidiform carpels which are clearly demarcated from the residual apex (fig. 25). In these stages the lateral faces of the adjoining carpels remain apart. Also later when the abaxial regions of the carpels grow upwards and start to overarch the adaxial regions, the lateral regions are still separate although they almost touch each other (fig. 26). Then the carpels adhere and fuse dermally leaving the space for the septal nectary and its widening epibasal opening (fig. 27). The styler parts grow by means of special apical activity which is dermal according to Hartl & Severin, and they also fuse later on. Finally, the ovaries have their late expansion, and also give rise to the epidermal flaps of tissue covering the openings of the nectaries (figs. 28, 29).

Dracaena surculosa

Daumann (1970) reported internal septal nectaries which open upwards on the upper part of the ovary.

Three hemispherical primordia arise in the corners of a triangular apex, leaving a residual apex in the middle (fig. 30). The primordia develop as ascidiform carpel primordia in the usual way, the abaxial regions leading, the lateral parts following, and the median adaxial side coming last (fig. 31). The carpel primordia are raised by the activity of a common basal meristem on their periphery. In that way the wall of a syncarpous ovary is formed. Then the abaxial part of the carpel primordium overarches the median adaxial part in a cap-like manner. The latter region gives rise to one median ovule (fig. 32). Furthermore the carpel primordia differentiate each into an ovarial part below and a styler-stigmatic part above, and then dermal fusion of these parts begins in a rather late phase. The lateral parts of the carpels fuse dermally

in the median as well as alternate radii, but leaving the spaces for the nectaries between them. Thus the spaces are delimited on the outside by the ovary wall which originated by meristematic fusion, and on the inside by the dermally fused regions (fig. 33). The radial spaces differentiate as nectaries that open high up on the ovary wall, and narrow grooves develop on the surface of the ovary by differential growth; these prolong the nectary openings downwards and may therefore serve for nectar guidance (fig. 34). In advanced stages the cells on top of the ovary above the nectary pores betray the epidermal fusion by a zigzag pattern. This irregular pattern is absent in the zone of meristematic continuity below the openings (fig. 35).

In *Sansevieria zeylanica* the development was very similar; the free carpel primordia also develop as ascidiform organs (fig. 36).

***Eichhornia paniculata* (Fig. 78)**

The peculiar location of the nectaries has been described by Daumann (1965). The three nectaries have pores at the base of the gynoecium from where the secreting internal spaces extend in the septa upwards.

Early stages show a triangular convex apex, along the slope of which three carpels originate free from each other in the corners (fig. 37). Soon afterwards the carpel primordia touch each other on their lateral faces, except basally (fig. 38), in that way preforming the pores of the nectary. Then the carpels grow markedly in height and attenuate upwards, differentiating the stylar-stigmatic part from the ovarial part. During this process the entire lateral faces fuse dermally where they touch, but the space for the septal nectary is secluded (figs. 39–41). Furthermore, the margins of the young carpels fuse dermally in the centre as usual, also in the stylar region.

Consequently, the position of the nectaries from the pores upwards is caused by the lack of meristematic fusion on the periphery of the gynoecium and by the concomitant upwards growth of the carpel primordia and the convex apex (fig. 37). The nectaries are bordered by the apex below and on the inside, and by dermally fusing sides of the carpels on the outside except at the base.

The development in *Pontederia cordata* is closely similar (figs. 42, 43).

***Hemerocallis fulva* (Fig. 79)**

The nectaries are located low down in the partly inferior gynoecium, for the greater part on a level below the locules. They open by distal slits on the base of the gynoecium just above the line of separation from the perianth (fig. 44). Later the nectary surface is slightly undulated. This description agrees with the report by Daumann (1970).

Very young stages show that the gynoecium originates on the slope of a triangular, slightly concave apex, which is bordered by the young stamens. The periphery of this apex grows upwards, slightly more so in the corners (figs. 45). Free carpel primordia grow inwards in the usual horseshoe-shaped fashion (fig. 46). At the same time the whole structure becomes more concave and extends in length (fig. 47).

The lateral parts of the carpels grow inwards and adhere. Also, the margins meet in the centre, adhere and fuse dermally. However, a space for the septal nectary is

left at the base between the carpel primordia. Thus the septal nectary is delimited on the outside by the concave floral apex, and on the inside by the dermally fused central parts of the carpels. The process of adherence and fusion continues as the gynoecium develops further in upward direction. The curious final position of the nectaries on a level below the locules is probably due to the initial difference in height between the median and alternate radii of the carpels on the concave apex. The regions in the septal radii of the gynoecium originate later than those in the median radii thus lower on the increasingly concave apex.

REMARKS ON THE DEVELOPMENT OF THE GYNOECIUM IN SOME SPECIES WITHOUT SEPTAL NECTARIES

***Bulbine annua* (Figs. 48–52)**

Early stages show that the gynoecium originates on the periphery of the floral apex as a triangular obtuse low ridge. As the sides grow inwards and the corner regions outwards, three carpels are demarcated. At first the entire primordial gynoecium grows upwards, but later intercarpellary regions slow down, so that stylar-stigmatic regions become distinct. As a consequence, in low transverse sections, septa appear as undivided parts. The septa are at first free from each other, but later after approaching the centre of the ovary fuse dermally. Also the stylar-stigmatic parts fuse dermally with each other into one style-stigma complex.

***Gloriosa superba* (Figs. 53–55)**

My observations agree mainly with the descriptions of the late stages by El Hamidi (1952), but in my opinion there are no ascidiate bases to the carpels.

The gynoecium arises as a peripheral, roughly triangular wall on the apex. This wall grows upwards as a whole, but as three corner regions slightly advance, three carpel regions can be distinguished. This primary stage is not followed by inward development of septa, but the gynoecium is modeled by proportional differences in growth between the locule regions in the corners and the alternating regions on the sides. As a result free lateral carpel parts occur, which later are adjacent in the alternate radii but do not fuse. Only the original marginal meristems of the carpels (by comparison) are primarily fused, as shown above. Later these three inward alternating parts (strictly no septa) fuse with each other dermally in the centre of the ovary, after the formation of rows of ovule primordia. The apically three-lobed stylar-stigmatic regions are sharply defined from the ovary parts later on.

***Veratrum nigrum* (Figs. 56–58)**

A description of late stages was given by El Hamidi (1952).

Young stages show that the carpels are fused by their margins in the lower part of the gynoecium from the beginning, but that the lateral parts of the carpels are free. Therefore I presume that *Veratrum* may be similar to *Gloriosa* in early development. However, in contrast with *Gloriosa*, the stylar-stigmatic parts of the gynoecium remain free later on. Half-way up, the carpel primordia have a slit-like section, where

the margins are free but adjacent in the centre; above, the margins diverge forming the stigmatic parts. The margins half-way up approach the centre, where they adhere and fuse dermally later. The ovule primordia originate submarginally, on the inner edge of the slit.

Salacca edulis (Figs. 59–64)

Occurrence of septal nectaries in palms is reviewed by Schmid (1983). In *Salacca* they are absent. Three carpels originate along the slope of the floral apex probably separately. Soon after, the primordia grow upwards together as a continuous broad peripheral gynoecial wall built around a triangular apex. On the corners the median carpel regions advance, followed by the fused parts on the sides. The latter parts may show a variable radial depression on the inside that indicates the border between the fused margins of two carpels. Centrally the floral apex develops into three fertile regions and a residual apex. The fertile regions are opposite to the median regions of the carpels (axillary), and give rise to one curving ovule each (Van Heel, 1977).

The whole young gynoecium is raised on a socle. The median parts of the carpels grow upwards and inwards and gradually narrow into stylar-stigmatic parts. The alternate septal parts grow inwards and later meet in the centre, adhering but not fusing. Their epidermal cells as well as those of the residual apex might be secretory. The lower stylar parts also meet in the centre but do not fuse; above they remain separate extending into stigmas. In young stages the stylar parts may still show the line demarcating the carpels on their inside.

DISCUSSION

The present small sample indicates the general way in which the spaces for the septal nectaries develop, and also shows the diversity of shape effectuated. Grassmann (1884) discovered that the spaces for the nectaries originate through lack of fusion between carpels. This view found wide acceptance. The definition given by Rudolf Schmid (1985) is in accordance, viz., 'a nectar-secreting cavity resulting from lack of intercarpellary postgenital fusion and lying in a septal radius.' In my opinion however, the initial free development of the carpels should be considered the precondition of the nectary spaces, followed by partial dermal fusion. This is because the nectaries originate laterally at the very base of free or partly free primordial carpels. A first differentiation into nectariferous cells could prevent the basal lateral epidermal cells of each primordium from fusing dermally with their neighbours like this occurs in epidermal cells above.

The role of free carpel development is also demonstrated by the absence of similar stages in gynoecia of Monocotyledons without septal nectaries. The septa may arise as one whole like in Dicotyledons. The development of the gynoecium in *Costus speciosus* may serve as a test-case. Three carpels are observed building up the roof of the inferior ovary, leaving outlets of two septal nectaries (fig. 65). The carpels originate free from each other where nectaries will differentiate, but fused where there will be none (fig. 66). In contrast with the Costaceae, the allied Zingiberaceae

do not have septal nectaries. Accordingly the septs turned out to arise fused in a *Globba* and an *Amomum* species investigated. Thus there is full correspondence between the presence of septal nectaries and free carpel development.

The very early morphogenesis of nectariferous epidermal cells at the lateral base of the carpels is a constant feature, whether the carpels remain free or are fused later. That may also constitute the argument for replacing the term septal nectary by gynopleural nectary as advanced by Smets & Cresens (1988).

Figures 71–79 show that the nectariferous areas in a gynoecium develop on the border between the apex or the continuous gynoeceal wall regions on one side and the free or later fused carpel regions on the other side, whatever their different forms and sizes. The morphological effects of these differences are reflected in Daumann's (1970) proposition of a phyletic line between 'outer' and 'inner' septal nectaries, depending on whether the nectaries are more concealed and the nectar secreted less directly to the outside. Outer nectaries are considered partly nectariferous grooves on the surface, being not the non-nectariferous secondary grooves that guide nectar away from the pores of inner septal nectaries. Schmid (1985) recognizes moreover confluent nectaries, which form an actual phylogenetic link between outer and inner septal nectaries.

Species with outer septal nectaries are rare; about ten cases have been recorded, and until now I have not investigated them by lack of appropriate material. Only my observations on *Tofieldia calyculata* show that the species has been listed incorrectly as having outer septal nectaries. Therefore all cases should be investigated developmentally. Until then I hold the transition from outer surface to gynopleural nectaries for unsettled. However, the nectaries of *Alisma* and especially *Butomus* may be considered 'confluent' nectaries, being almost open to half-concealed 'septal' or rather gynopleural nectaries. These aspects will be fully discussed by Rudolf Schmid in his forthcoming review.

The difference in location and shape of the nectaries, here discussed, also depends on the degree of syncarpy by meristematic continuity (sensu Sattler, 1978). Continuity describes the outcome of a process which can be observed during development. The process comprises changing interrelations between meristems in place and time of origin in several systematically related taxa. The height of the openings of the nectaries on the gynoecium can be defined by the degree of syncarpy. In *Tofieldia* and *Eichhornia* such syncarpy is absent and the openings are basal, in *Ornithogalum* syncarpy is considerable and the openings are distal. In *Arenga*, the height of the openings increases during later development. The possible disadvantage of high openings for the fixation of the nectar may be offset by the secondary development of nectar guiding grooves on the surface of the ovary.

The occurrence of syncarpy exclusively along the periphery of the gynoecium may be explained by the late intervention of meristematic continuity with the development of the carpel primordia. When syncarpy intervenes late horseshoe-shaped carpel primordia meet laterally and grow upwards together on that location. The inward horseshoe parts, being already formed, remain free, creating a space where a

nectary may differentiate at the base. This condition has been called the hemisynplicate type of gynoecium by Leinfellner (1950). However, I think Leinfellner has not realized the strict relation with septal nectaries, as did much later Hartl & Severin (1981). When syncarpy occurs early, the horseshoe-shaped formations have not yet progressed very far. In that case a 'straight' gynoecium wall originates directly, and if septa grow inwards they do so directly as one whole, leaving no space for septal nectaries, but effectuating a quick and firm syncarpous construction.

Supposedly nectaries could develop also on the border between continuous septa and the free parts above. But then they would be no longer septal, though gynopleural. Maybe some of the reported outer septal nectaries fall under this heading. Also Zingiberaceae (and *Buxus*) may fit this category. The remarkable transitions in the nectaries of Burmanniaceae as described by Rübsamen (1986) are important here also.

Above it has been demonstrated that the occurrence of septal nectaries is associated with free or partly free carpels. For that reason I consider septal nectaries as original in Monocotyledons, accepting the theory that free carpels are original in Angiosperms generally, and fused carpels came later. I have not found a changing developmental mechanism suggestive of secondary apocarpy as an adaptation to septal nectaries.

This view is not in favour of a general acropetal evolutionary direction in the occurrence of nectaries in the flower as a whole, as proposed by Fahn (1953, 1979) and accepted by Daumann (1970). The distinction of the Asparagales and Liliales within the Liliiflorae, among other reasons based on the presence or absence of septal nectaries, is supported (Dahlgren, Clifford & Yeo, 1985). The opinion that the absence of septal nectaries or the replacement by other nectaries is a derived condition (Dahlgren & Rasmussen, 1983) is also supported.

In conclusion it can be said that septal nectaries develop by three successive events: 1) the origin of free or incipient syncarpous carpels, on the lateral base of which the epidermis starts differentiating into secretory cells, 2) the definition of the ultimate shape of the nectary by variable upgrowth of the apex and the continuous wall of the gynoecium on one side, and the dermal fusion of carpellary parts on the opposite side, 3) the addition of features as undulated secretory surfaces, septal grooves, etc.

REFERENCES

- BAUM, H. 1949. Zur Frage des schrittenweisen Überganges vom apokarpen zum coenokarpen Gynözeum. *Österr. Bot. Zs.* 95: 470–474.
- BÖHMKE, 1917. Beiträge zur Kenntnis der floralen und extrafloralen Nektarien. *Beih. Bot. Centralbl.* I, 33: 169–247.
- DAHLGREN, R. M. T., & H. T. CLIFFORD. 1982. The Monocotyledons: a comparative study. In: V. H. Heywood (ed.), *Botanical Systematics 2*. Academic Press.
- , H. T. CLIFFORD & P. F. YEO. 1985. The families of the Monocotyledons. Structure, evolution, and taxonomy. Springer.
- & F. N. RASMUSSEN. 1983. Monocotyledon evolution. Characters and phylogenetic estimation. *Evolutionary Biology* 16: 255–395.

- DAUMANN, E. 1964. Zur Morphologie der Blüte von *Alisma plantago-aquatica* L. *Preslia* 36: 226–239.
- 1965. Das Blütennektarium bei den Pontederiaceen und die systematische Stellung dieser Familie. *Preslia* 37: 407–412.
- 1970. Das Blütennektarium der Monocotyledonen unter besonderer Berücksichtigung seiner systematischen und phylogenetischen Bedeutung. *Feddes Repertorium* 80: 463–590.
- EBER, E. 1934. Karpellbau und Plazentationsverhältnisse in der Reihe der Helobiae. *Flora NF* 27: 273–330.
- EL HAMIDI, A. 1952. Vergleichend-morphologische Untersuchungen am Gynoeceum der Unterfamilien Melanthioideae und Asphodeloideae der Liliaceae. Arbeiten aus dem Institut für Allgemeine Botanik an der Universität Zürich. Ser. A, no. 4: 1–50.
- FAHN, A. 1953. The topography of the nectary in the flower and its phylogenetical trend. *Phytomorphology* 3: 424–426.
- 1979. *Secretory tissues in plants*. Academic Press.
- GRASSMANN, P. 1884. Die Septaldrüsen, ihre Verbreitung, Entstehung und Verrichtung. *Flora* 67: 113–136.
- HARTL, D., & I. SEVERIN. 1981. Verwachsungen im Umfeld des Griffels bei *Allium*, *Cyanastrum* und *Heliconia* und den Monokotylen allgemein. *Beitr. Biol. Pflanzen* 55: 235–260.
- HEEL, W. A. VAN. 1977. On the morphology of the ovules in *Salacca* (Palmae). *Blumea* 23: 371–375.
- 1981. A S.E.M.-investigation on the development of free carpels. *Blumea* 27: 499–552.
- 1983. The ascidiform early development of free carpels, a S.E.M.-investigation. *Blumea* 28: 231–270.
- 1984. Variation in the development of ascidiform carpels, an S.E.M.-investigation. *Blumea* 29: 443–452.
- HIDAJAT, E. B. 1976. Morphology and anatomy of the inflorescence axis and flowers in *Arenga porphyrocarpa* (Palmae). *Proceedings Institute of Technology Bandung* 11: 23–38.
- 1987. Flowering behavior in the Sugar Palm, *Arenga pinnata*. *Principes* 31: 78–88.
- LEINFELLNER, W. 1950. Der Bauplan des synkarpen Gynözeums. *Österr. Bot. Zeitschr.* 97: 403–436.
- RÜBSAMEN, T. 1986. Morphologische, embryologische und systematische Untersuchungen an *Burmanniaceae* und *Corsiaceae* (Mit Ausblick auf die *Orchidaceae-Apostasioideae*). *Diss. Bot.* 92: 1–310.
- SATTLER, R. 1978. 'Fusion' and 'Continuity' in floral morphology. *Notes Roy. Bot. Gard. Edinburgh* 36: 397–405.
- SCHMID, R. 1970. Notes on the reproductive biology of *Asterogyne martiana* (Palmae). *Principes* 14: 1–9 (Part I) and 3–49 (Part II).
- 1983. Septal nectaries of *Asterogyne martiana* and other Palmae. *Principes* 27: 168–174.
- 1985. Functional interpretations of the morphology and anatomy of septal nectaries. *Acta Bot. Neerl.* 34: 125–128.
- SINGH, V., & R. SATTLER 1974. Floral development of *Butomus umbellatus*. *Can. J. Bot.* 52: 223–230.
- SMETS, E. F., & E. M. CRESENS. 1988. Types of floral nectaries and the concepts 'character' and 'character-state'. A reconsideration. *Acta Bot. Neerl.* 37: 121–128.
- STERLING, C. 1979. Comparative morphology of the carpel in the Liliaceae: Tofieldieae. *Bot. J. Linnean Soc.* 79: 321–332.
- TILTON, V. R., & H. T. HORNER. 1983. Carpel development, anatomy, and function in the reproductive process in *Ornithogalum caudatum* (Liliaceae). *Flora* 173: 1–31.
- UHL, N. W., & H. E. MOORE. 1971. The palm gynoeceum. *Amer. J. Bot.* 58: 945–992.
- WILDE-DUYFJES, E. E. DE. 1976. A revision of the genus *Allium* L. (Liliaceae) in Africa. Thesis, Wageningen.

REMARKS AT THE FIGURES

The photographs of each species are presented at equal magnification or at easily comparable magnifications. In that way the primordia can be better visualized as growing structures. As a consequence, however, photographs of different sizes result. All scale bars represent 0.1 mm, unless indicated otherwise. Abbreviations: s.n. in the explanations means septal nectary; transverse section: t.s.; longitudinal section: l.s.

Fig. 1. *Alisma plantago-aquatica*. Lateral view on two carpels. Arrow indicates place of nectary. — Fig. 2. *Butomus umbellatus*. Common growth of young carpels at the base. — Figs. 3–5. *Tofieldia calyculata*. — 3: Ascidiiform carpel primordia; 4: detail showing basal common nectary space (arrow); 5: older gynoecium, one carpel removed; arrows point at openings of two s.n. — Fig. 6. *Arenga pinnata*. Gynoecium primordium with socle, lines of dermal fusion above the openings of the s.n.

Figs. 7–8. *Arenga pinnata*. — 7: Gynoecium primordium, one carpel isolated. Above the s.n. space (arrow) a disruption of cells shows where dermal fusion of carpels has begun; 8: pistil after flowering (LM); arrows point at openings of s.n. — Figs. 9–12. *Asphodelus fistulosus*. Gynoecium development. — 12: Spaces of s.n. between ascidiiform carpels.

Figs. 13–16. *Asphodelus fistulosus*. — 13: Peripheral upgrowth of gynoecium; 14: one carpel removed; adaxial bases of carpels are demarcated from the residual apex; spaces of s.n. between the flanks of carpels; 15: one carpel removed; disrupted cells show where dermal fusion starts bordering the s.n. space on the inside (arrows), peripheral upgrowth occurs on the outside; 16: development of aril on ovule primordium, and growth of protuberant cells on carpel margins above the ovules.

Fig. 17. *Asphodelus fistulosus*. Dorsal part of carpel removed; s.n. shows at the bottom left; ovules have aril, outer and inner integument; U-shaped placenta with protuberant cells. — Figs. 18–22. *Ornithogalum caudatum*. — 18: Gynoecium with nectar-guiding grooves; 19: young 'hemisynpicate' primordium; 20: meristematic continuity on the periphery and separate carpels on the inside; 21: late stage; the s.n. is bordered by dermal fusion on the inside; 22: t.s. of gynoecium wall just below the confluence of s.n. and external groove.

Fig. 23. *Kniphofia spec.* Gynoecium primordium, one carpel removed. Meristematic fusion at the periphery, but distinct margins of the carpels on the inside. — Figs. 24–27. *Allium fistulosum*. — 24 & 25: Origin of distinct ascidiiform carpels; 26: abaxial upgrowth of carpels, and origin of the spaces for s.n. between them; 27: development of the style; in sutural radii occurrence of common meristematic growth basally, and epidermal fusion above; between these two zones the openings of the s.n. are evident.

Figs. 28 & 29. *Allium fistulosum*. — 28: Longitudinal section of s.n. and its outlet; 29: surface view of outlet. — Figs. 30–33. *Dracaena surculosa*. — 30: Flower primordium with petals, stamens and the initiation of three carpels; 31: gynoecium primordium with three ascidiiform carpels which show peripheral continuity and the beginning of the space for the s.n.; 32: l.s. of slightly older stage; 33: the same stage, seen from the outside.

Figs. 34 & 35. *Dracaena surculosa*. — 34: Young gynoecium, in part removed, showing space for s.n. (arrow) and external issuing groove; 35: ovary at anthesis showing openings of the s.n. and the groove downwards; note lines of dermal fusion above the openings. — Fig. 36. *Sansevieria zeylanica*. One carpel removed. Base of two distinct ascidiiform carpels. The space for s.n. shows between the carpels. — Figs. 37–39. *Eichhornia paniculata*. — 37: Origin of three distinct carpels; 38: older stage; the carpels are adjacent except at the base (arrow) where the mouth of the s.n. is formed; 39: older stage; dermal fusion of the carpels begins above the mouth of the s.n.

Figs. 40 & 41. *Eichhornia paniculata*. Increasing dermal fusion of carpels in two older stages of gynoecium. Opening of the s.n. at the base (arrow). — Figs. 42 & 43. *Pontederia cordata*. — 42: Primordial gynoecium showing three carpels laterally adjacent except at the base; arrow points at future mouth of s.n.; 43: young gynoecium showing openings of s.n. with the line of dermal fusion above. — Figs. 44–47. *Hemerocallis fulva*. — 44: Young, slightly inferior ovary showing space of s.n. at the base left; 45: primordial flower with two of the petals, the stamens, and a concave gynoecial apex; 46 & 47: development of distinct but adjacent carpels on the concave apex.

Figs. 48–51. *Bulbine annua*. Early development of gynoecium. — 48 & 49: Carpels originate together as a roughly triangular rim on the apex; 50: septa grow inwards, and stylar-stigmatic upper halves become distinct; 51: slightly older stage, no s.n.

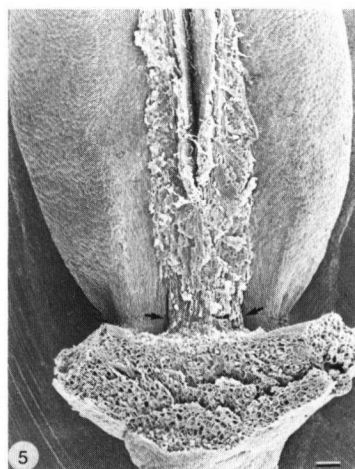
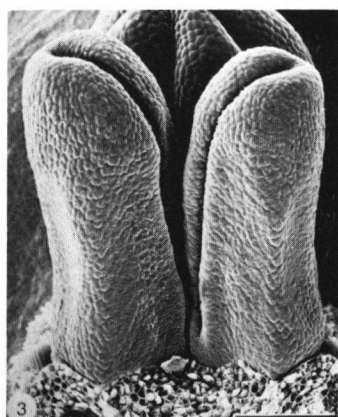
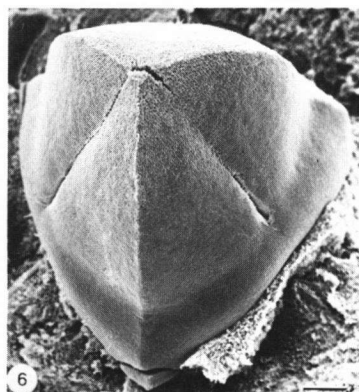
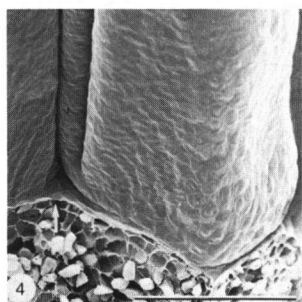
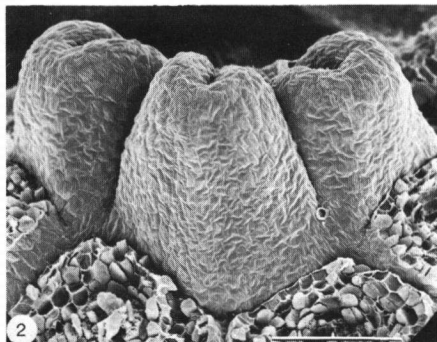
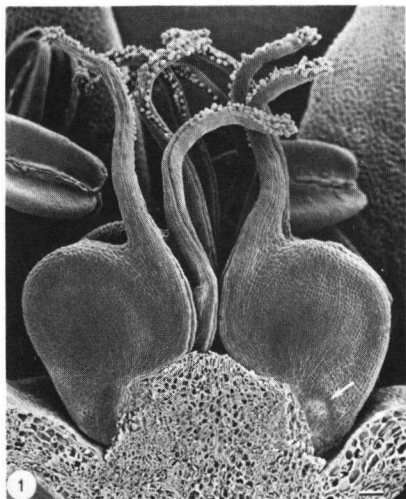
Fig. 52. *Bulbine annua*. Gynoecium before anthesis. No s.n., but distal hairs on filaments. — Figs. 53–55. *Gloriosa superba*. — 53: Origin of three fused carpels; 54: sutural parts grow inwards, locular regions outwards; 55: dermal fusion of sutural parts in the centre; ovule primordia. — Figs. 56 & 57. *Veratrum nigrum*. — 56: Young gynoecium, in part removed. Sutural regions grow inwards, fused in the lower halves. Ovary regions grow outwards, bearing ovule primordia on the inner edge of the slit; 57: older stage from outside, no s.n.

Fig. 58. *Veratrum nigrum*. Young gynoecium, upper half of one carpel removed. Protuberant cells on the border of ovary part and stylar-stigmatic part. — Figs. 59–62. *Salacca edulis*. — 59: Origin of three carpels; 60: development of gynoecium wall by meristematic fusion of the carpels; 61: ibidem, septal grooves on the inside; origin of three axillary ovules; 62: young gynoecium from outside, differentiation of ovary part and stylar-stigmatic part; no s.n.

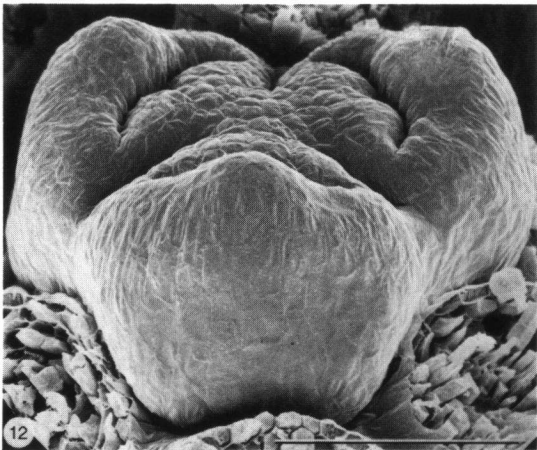
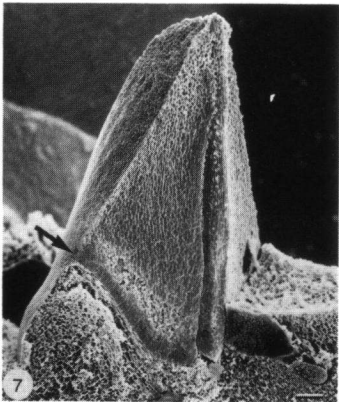
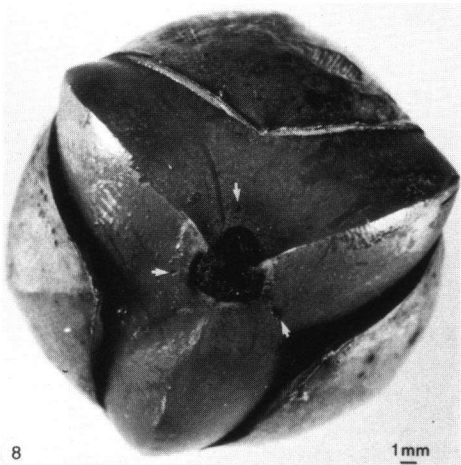
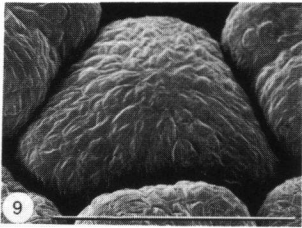
Figs. 63 & 64. *Salacca edulis*. — 63: About the same stage as in 62, but seen from inside and in part removed; septal part grows inwards over the apex; apex shows two of the axillary ovules; socle of gynoecium is evident; 64: older stage, the stylar-stigmatic part is attenuating, a septal groove is slightly visible. — Figs. 65 & 66. *Costus speciosus*. 'Roof' of inferior gynoecium. — 65: two outlets of the two s.n. (arrows), stylar tube in the middle; 66: primordial stage of the same, the carpels are fused medianly, but are distinct where s.n. will develop.

Figs. 67–70. *Tofieldia calyculata*. Transverse section of gynoecium (in part) in upward sequence. — 67: Base of gynoecium in the centre of the slightly concave receptaculum; the carpels are distinct centrally and have nectariferous epidermides; 68: bases of carpels fully distinct, with nectariferous epidermides; carpel dorsal vascular bundles branch off; 69: t.s. of basal region of the locules cutting through the upper inner part of the common s.n.; 70: t.s. of basal placental region above the s.n.; the lateral carpel surfaces start epidermal fusion.

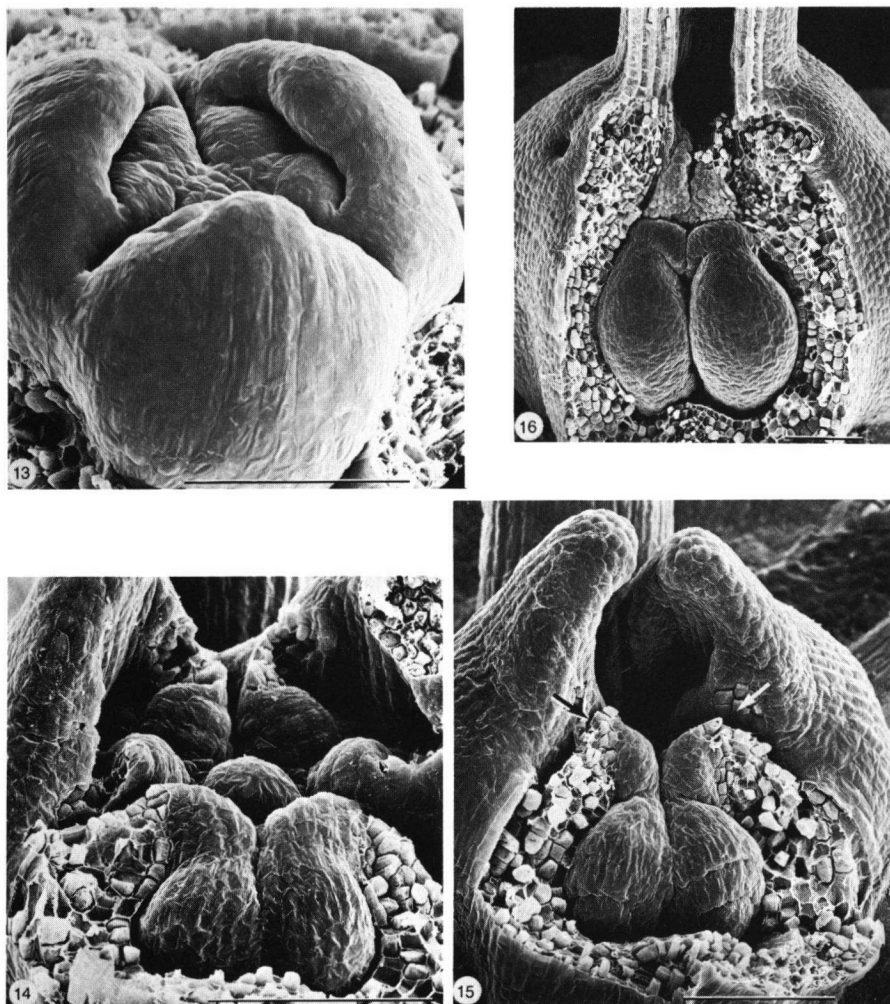
Figs. 71–79. Schematic presentation of l.s. of septal radii of gynoecia (on the left); showing s.n. (black), apex or meristematic continuity (dotted), and areas of dermal fusion (lined). On the right the locular radii are given (as if) in the same plane. — 71: *Alisma plantago-aquatica*; 72: *Butomus umbellatus* (arrow: slit area); 73: *Tofieldia calyculata*; 74: *Arenga pinnata* (arrow: increasing upward growth); 75: *Asphodelus fistulosus*; 76: *Ornithogalum caudatum* (arrow: external groove); 77: *Alilium fistulosum*; 78: *Eichhornia paniculata*; 79: *Hemerocallis fulva*.



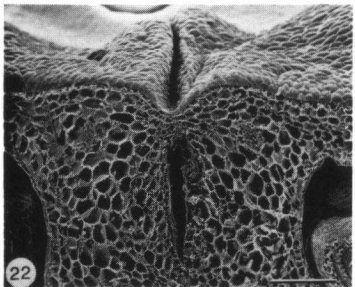
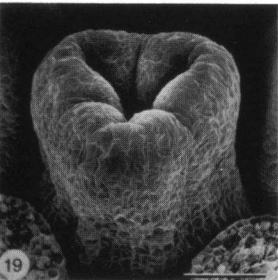
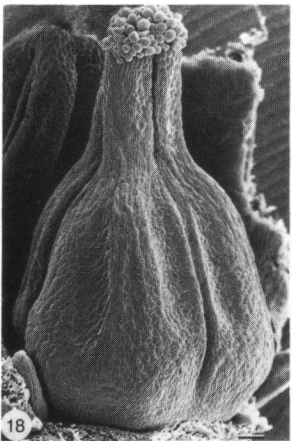
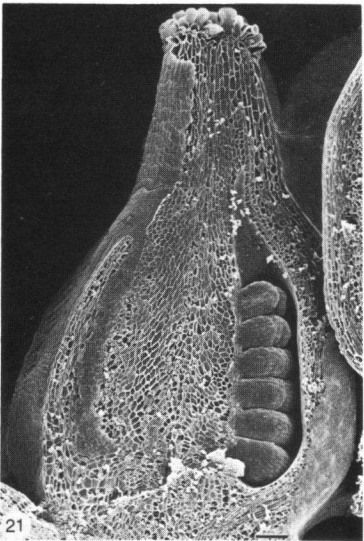
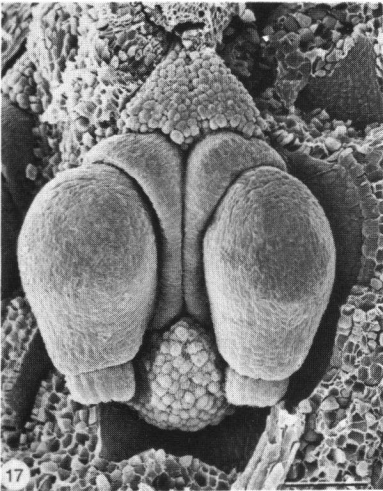
Figures 1–6



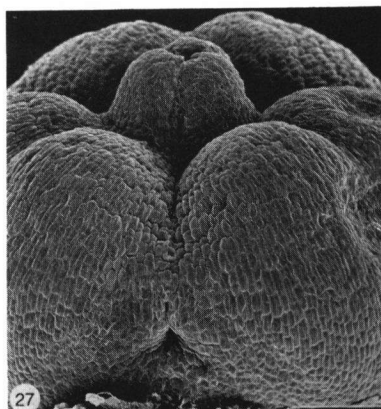
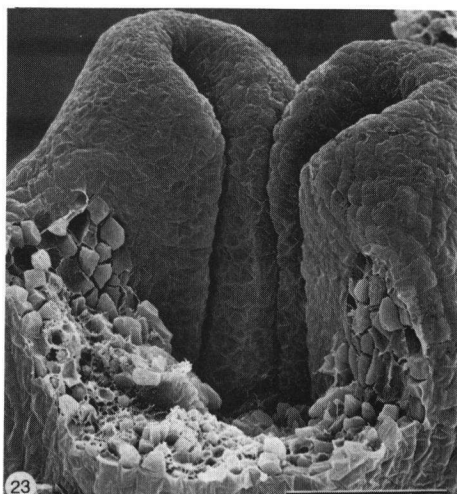
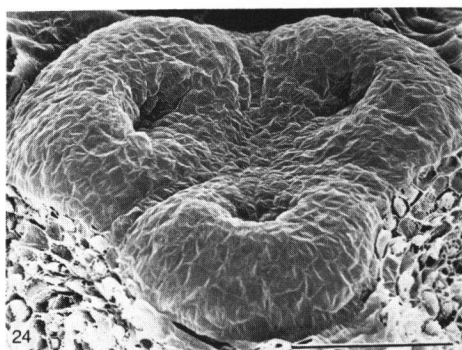
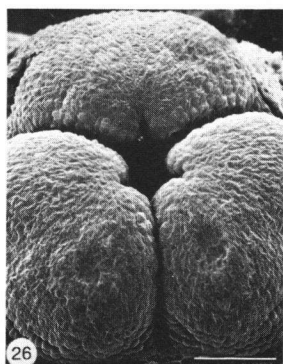
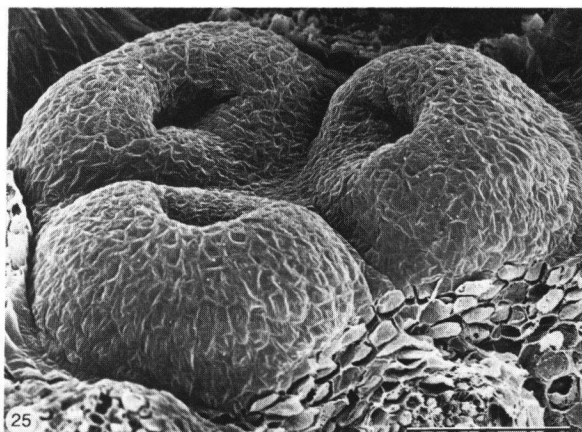
Figures 7-12



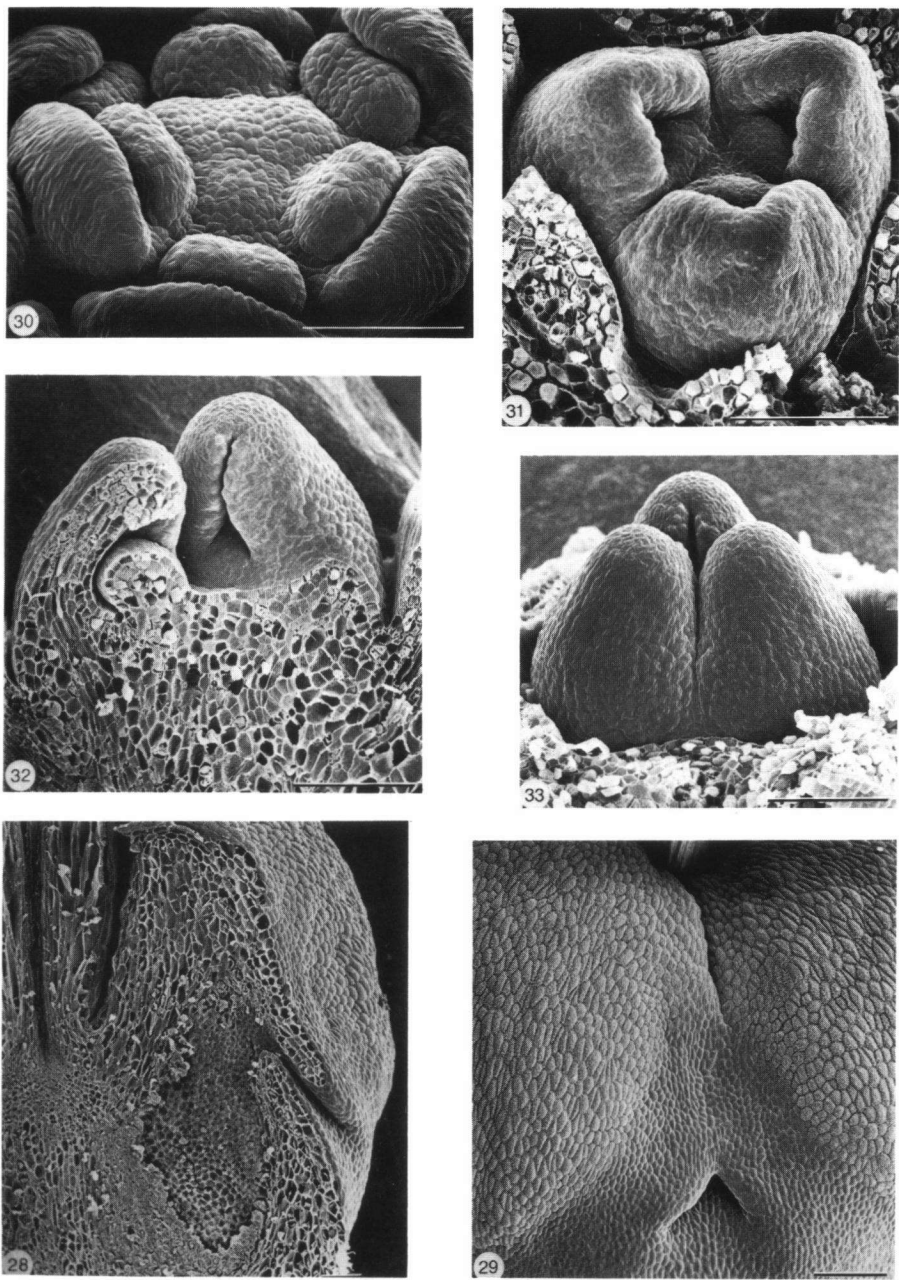
Figures 13–16



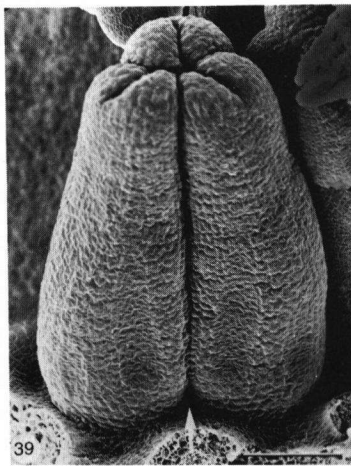
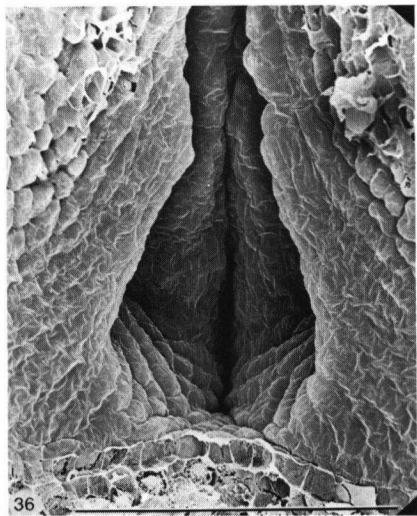
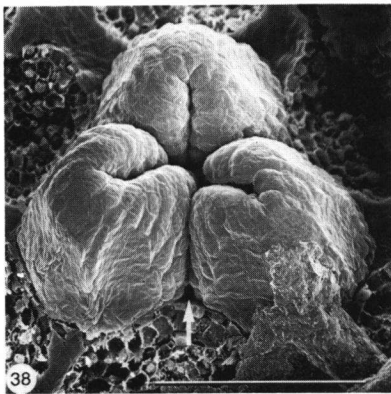
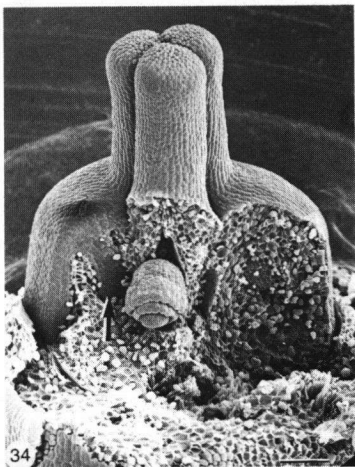
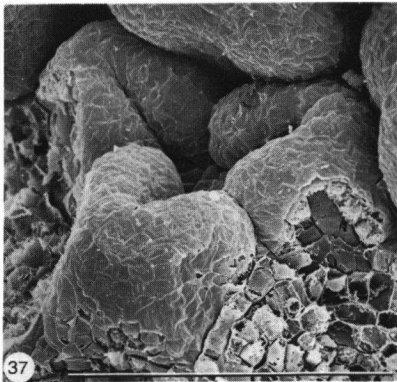
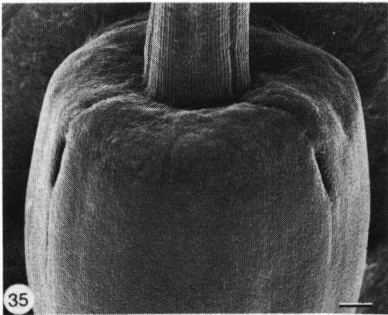
Figures 17–22



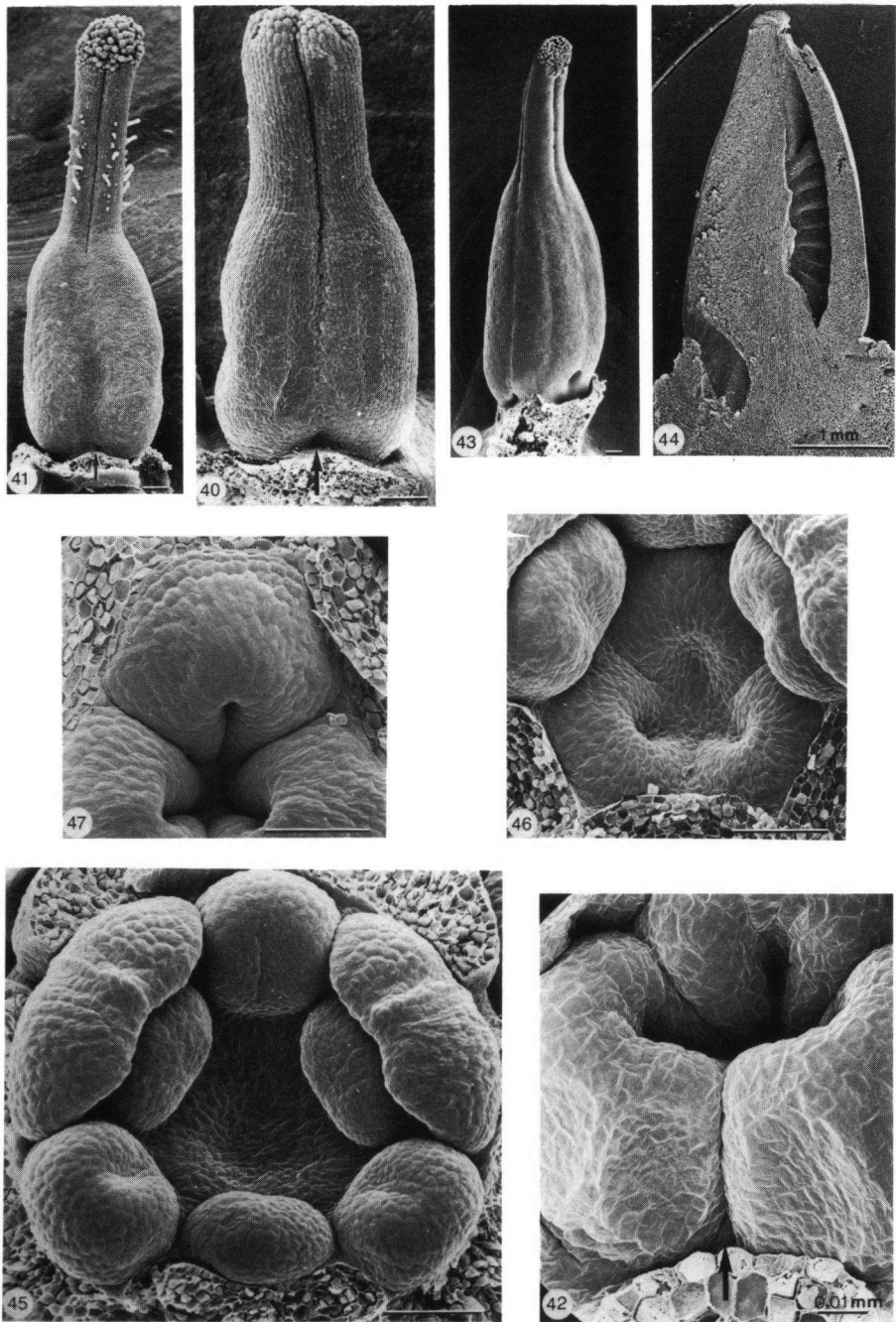
Figures 23–27



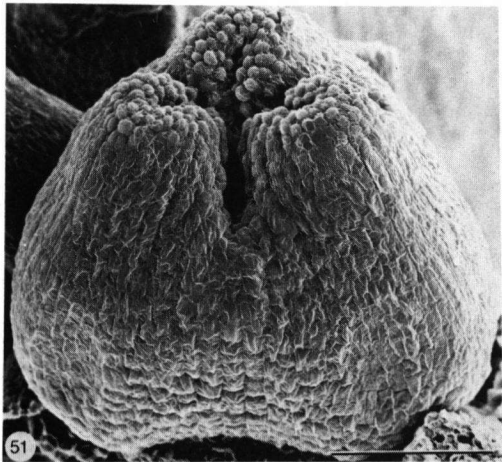
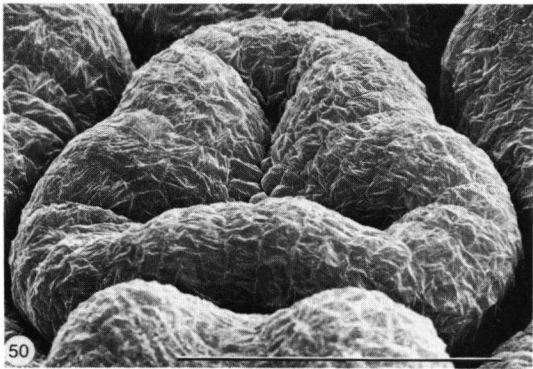
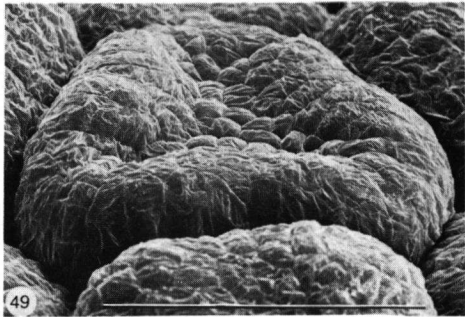
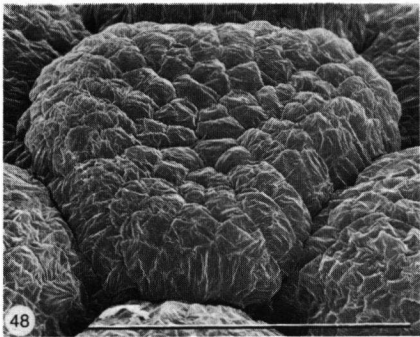
Figures 28–33



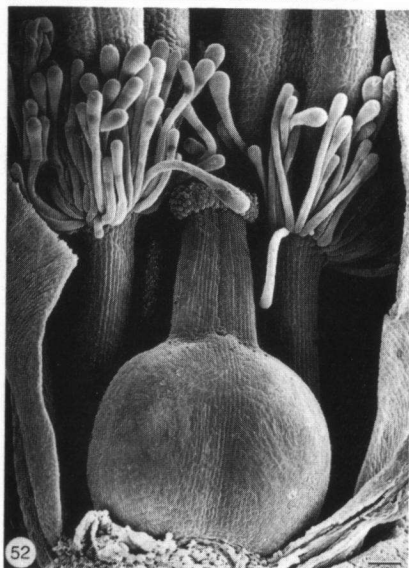
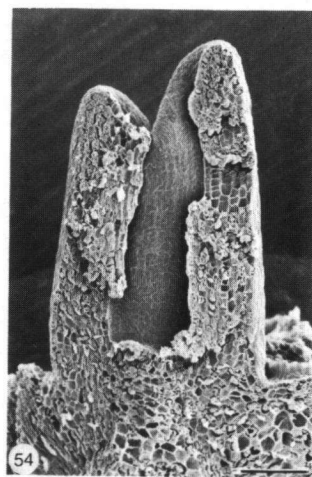
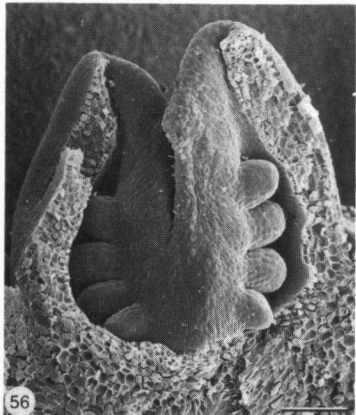
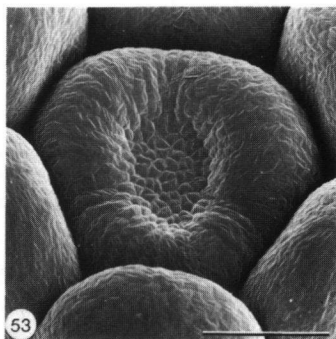
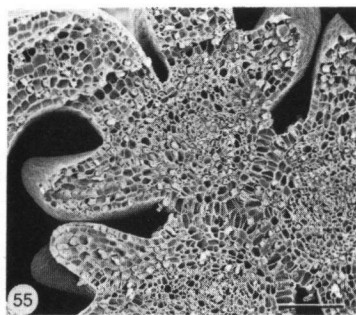
Figures 34–39



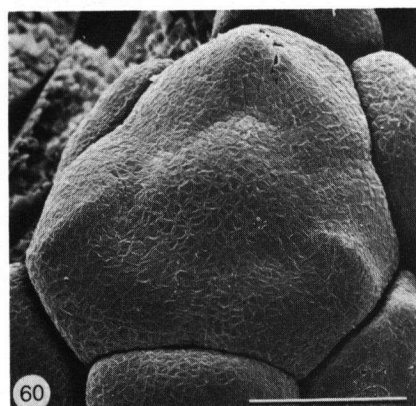
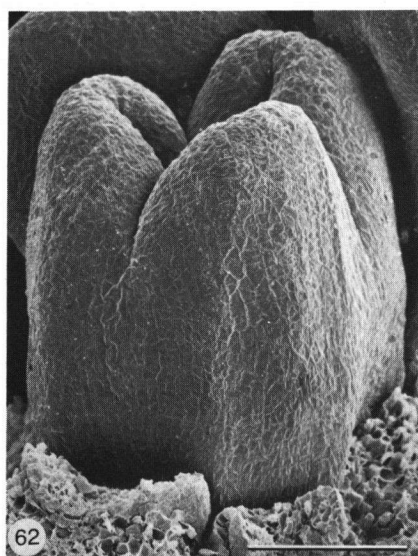
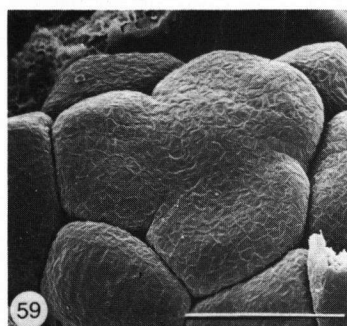
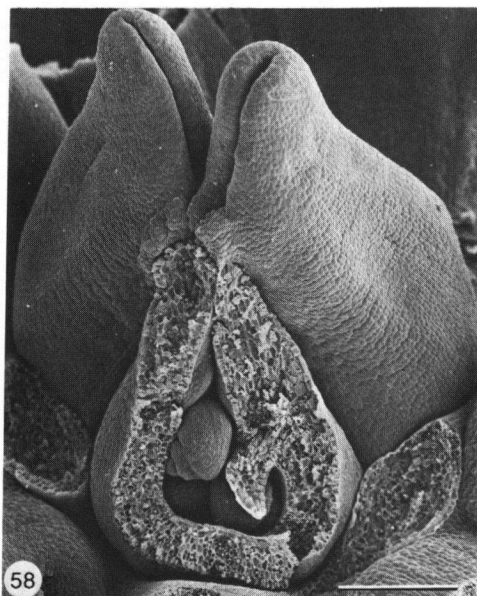
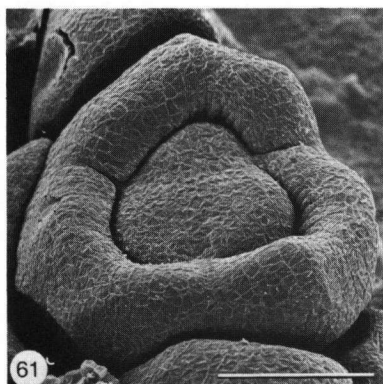
Figures 40-47



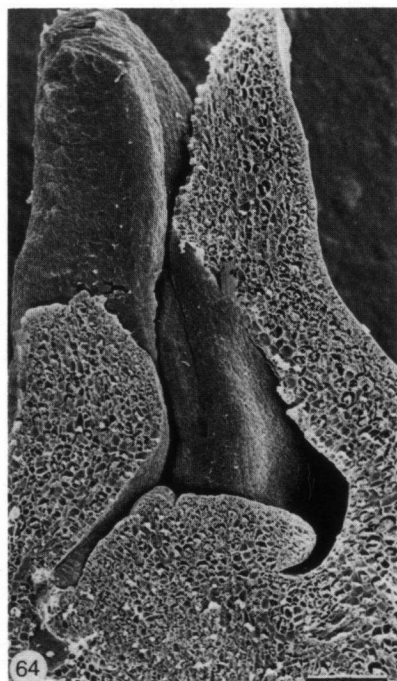
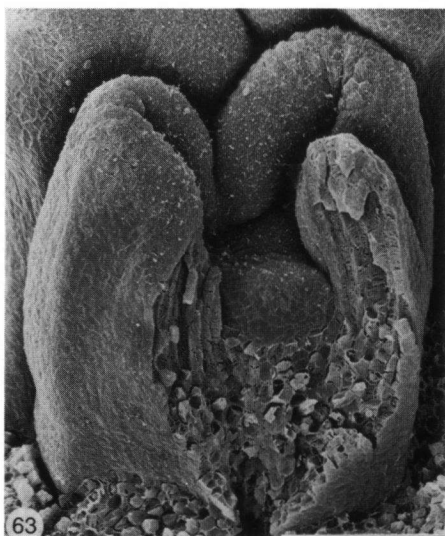
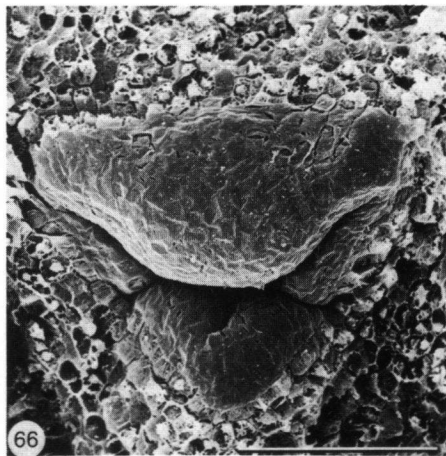
Figures 48–51



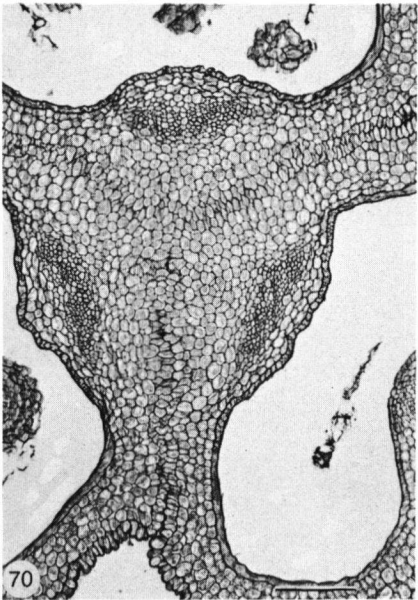
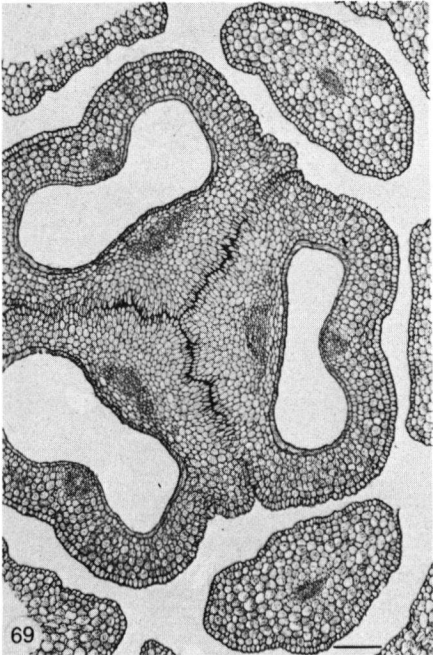
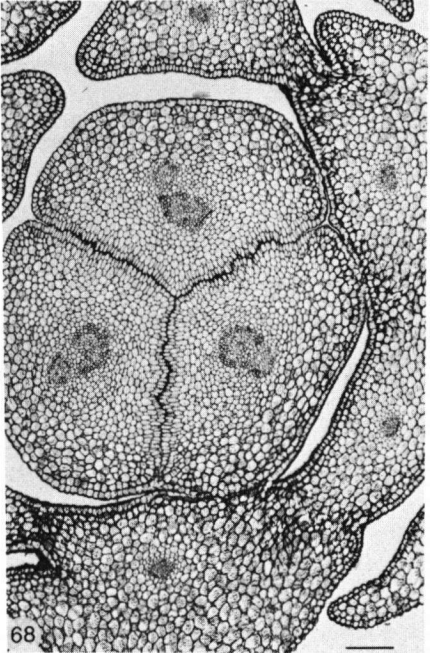
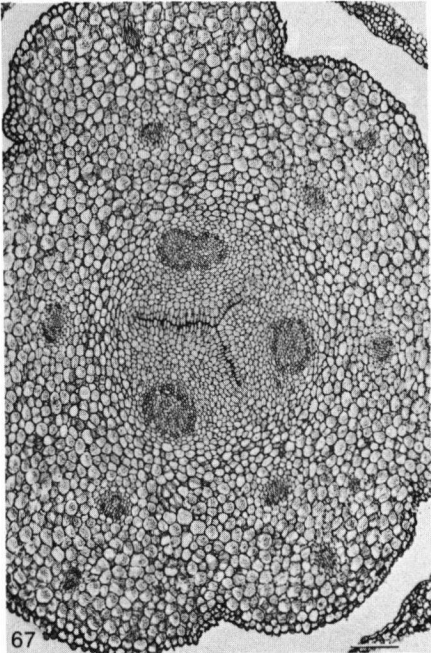
Figures 52–57



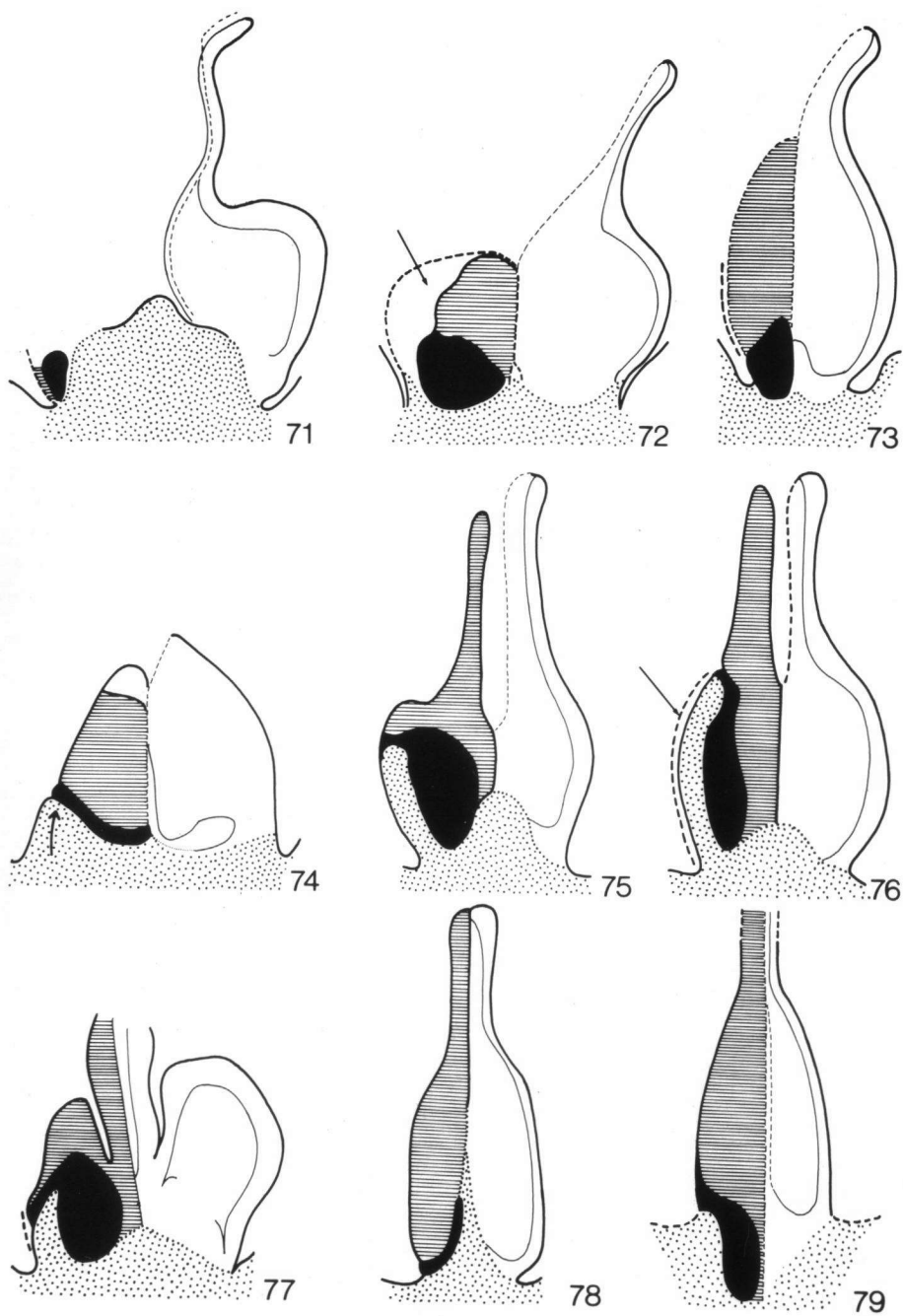
Figures 58–62



Figures 63–66



Figures 67-70



Figures 71-79